

Current Biology

Food for Sex in Bats Revealed as Producer Males Reproduce with Scrounging Females

Highlights

- Egyptian fruit bats form seasonal bonds through producer-scrounger interactions
- Genetic paternity tests of pups were used to examine the food-for-sex hypothesis
- Females mate with males from which they scrounge food
- Each female scrounges from a unique set of preferred males, and no male prevailed

Authors

Lee Harten, Yosef Prat,
Shachar Ben Cohen, Roi Dor,
Yossi Yovel

Correspondence

yossiyovel@gmail.com

In Brief

Harten et al. follow the social foraging activity of a captive colony of Egyptian fruit bats. They use genetic paternity analysis of pups to reveal that producer-scrounger interactions promote reproductive intersexual relationships. These findings demonstrate an interesting case of food-for-sex reciprocity in a social mammal.

Food for Sex in Bats Revealed as Producer Males Reproduce with Scrounging Females

Lee Harten,^{1,3} Yosef Prat,^{1,3} Shachar Ben Cohen,¹ Roi Dor,¹ and Yossi Yovel^{1,2,4,*}

¹School of Zoology, Faculty of Life Sciences, Tel Aviv University, 6997801 Tel Aviv, Israel

²Sagol School of Neuroscience, Tel Aviv University, 6997801 Tel Aviv, Israel

³These authors contributed equally

⁴Lead Contact

*Correspondence: yossiyovel@gmail.com

<https://doi.org/10.1016/j.cub.2019.04.066>

SUMMARY

Food sharing is often evolutionarily puzzling, because the provider's benefits are not always clear. Sharing among kin may increase indirect fitness [1], but when non-kin are involved, different mechanisms were suggested to act. Occasionally, "tolerated theft" [2, 3] is observed, merely because defending a resource is not cost effective. Sharing may also be explained as "costly signaling" [4, 5], where individuals signal their high qualities by distributing acquired resources, as has been suggested to occur in certain human cultures [6]. Alternatively, a transferred food item might be compensated for in later interactions [7]. In vampire bats, blood sharing reflects reciprocity between non-kin colony members [8–10], and long-term social bonds affect food sharing in chimpanzees [11]. Food may also be exchanged for other goods or social benefits [12–14]. One reciprocity-based explanation for intersexual food sharing is the food-for-sex hypothesis [15–17]. This hypothesis proposes that males share food with females in exchange for mating opportunities. Studies on human hunter-gatherer societies suggest that males with increased foraging success have higher reproductive success [18, 19]. Male chimpanzees, which in contrast to humans do not maintain pair bonds, were suggested to share food with females to increase their mating opportunities [16] (but see [20]). Bats, which are long-lived social mammals [21, 22], provide an opportunity to study long-term social reciprocity mechanisms. We monitored producer-scrounger interactions of a captive Egyptian fruit bat (*Rousettus aegyptiacus*) colony for more than a year and genetically determined the paternity of the pups that were born in the colony. We found that females carry the young of males from which they used to scrounge food, supporting the food-for-sex hypothesis in this species.

RESULTS

Egyptian fruit bats are social mammals that live in colonies of dozens to thousands of individuals for dozens of years. These bats have previously been shown to have clear individual preferences for one of two foraging strategies: either acquiring food on their own ("producing") or obtaining food from the mouth of another individual ("scrounging") [23]. During foraging, approaching another bat in an attempt to retrieve food appears as a typical act of scrounging (Video S1); thus, we will use this term hereafter, although we later show its reciprocal properties (see below). Females are more likely to initiate foraging interactions, approaching the producers in an attempt (often aggressively) to take food from their mouth. Males, which are more frequently the "producers" of food items, can act aggressively toward scrounging attempts and thus shape their affiliation with specific females in the long run. Furthermore, while foraging, captive scrounging bats exhibit persistent preferences of interaction partners over time [23]. Males usually initiate mating, but females can be highly aggressive in response to mating attempts and seem to control whom they copulate with [24]. Female Egyptian fruit bats give birth to a single pup after a gestation period of ca. 4 months, up to twice a year. Parturition is relatively synchronized around two main mating seasons. In nature, parturition usually peaks around March and September, and most pups are born within 2 months of these peaks. We saw a similar pattern in our colony, with slightly more spread that could be a result of captivity. The study colony was inhabited by 15 adult males and 10 adult females (and pups that were born during the monitoring period; see STAR Methods), making it similar to a small natural colony. We recorded the producer-scrounger interactions in the colony for 16 months (March 2015–July 2016).

Measurement of Scrounging Specificity in Producer-Scrounger Interactions

We measured the scrounging specificity of all pairs in our colony by considering the incidence of each individual approaching each of the other individuals for obtaining food (scrounging). This allowed us to reconstruct the producing-scrounging social network of our colony, in which the strength of each directed network link between a pair of individuals was proportional to

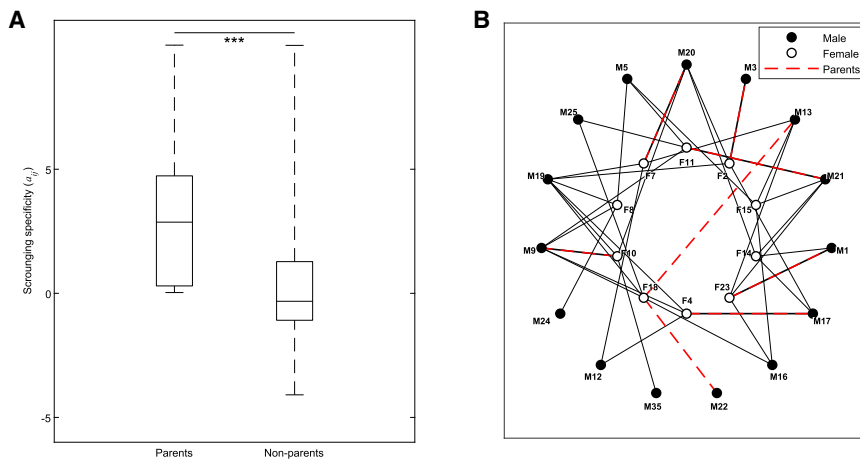


Figure 1. Scrounging Specificity and Reproduction

(A) The scrounging specificity between females and males that have reproduced during the monitoring period (parents; $n = 8$ pairs) and those pairs that have not reproduced during the same period (non-parents; $n = 142$ pairs). The parents' score is significantly higher than the non-parents' score ($p = 0.001$; permutation test; see text for details). (B) The producer-scrounger network of the bat colony. Each female (white circles) is connected to her top four associated males (black circles), according to her scrounging specificity. Red dashed lines depict a reproductive bond during the monitoring period. Note that 6 out of the 8 pups were born to pairs that are connected in this producer-scrounger network (only two red dashed lines do not align with a black edge in the graph).

the number of events in which one peer scrounged food from the other (see STAR Methods for details). We normalized the link strength by the propensity of each individual to use different foraging strategies (i.e., producing or scrounging). To this end, for each pair of individual bats i and j , we calculated a scrounging-specificity score a_{ij} as follows:

$$a_{ij} = \frac{s_{ij} - \mu_{ij}}{\sigma_{ij}}, \quad (\text{Equation 1})$$

where s_{ij} is the number of observed scrounging events of bat i from bat j and μ_{ij} and σ_{ij} are the mean and SD of the expected scrounging events between the same two bats (i from j), given their propensity to use either strategy (producing or scrounging; see STAR Methods).

Producer-Scrounger Pairs Mate and Reproduce

To examine whether producer-scrounger bonds are related to mate selection, we determined the paternity of the pups that were born during a period of 2.5 years starting right before the social-monitoring period and ending ca. 1 year after it, covering a total of ca. 6 reproduction periods (*R. aegyptiacus* typically reproduces twice a year) [23]. All in all, 24 pups were sampled, and for 18 pups, both parents could be identified (see STAR Methods). Genetic analysis also confirmed that there was no relationship between the adult bats in the colony [23]. During the period in which we monitored producer-scrounger interactions, eight of the 10 females in the colony gave birth. We evaluated the scrounging-specificity scores (a_{ij} , where female i scrounge food from male j) of the parents of these eight pups and found that the scrounging specificity of pairs that reproduced during the monitoring period was significantly higher than that of pairs that have not reproduced ($p = 0.001$; permutation test; Figure 1A). Therefore, foraging interactions were strongly related to mate choice. Figure 1B depicts the network of female-male scrounging specificity, where only the top four scrounging associations with males, for each female, are shown (we chose the four strongest associations because their scrounging specificity was, on average, higher than one: $a_{ij} > 1$). Six out of the eight pups conceived during the monitoring period were produced by pairs, which are connected in this network, that is, by pairs that were

among the top four scored according to their producer-scrounger interactions (black lines in Figure 1B depict the 4 highest scrounging-specificity scores of each female, and red dashed lines depict pairs that reproduced; note that 6 of the 8 red lines coincide with black lines; $p = 0.004$; exact test). The two reproducing pairs that do not coincide with this producer-scrounger network include one female that gave birth twice during the monitoring period and thus may have shifted her preferences during the experiment (see below).

This presentation also demonstrates an almost uniform distribution of producer-scrounger interactions and mating preferences. None of the males fathered more than a single pup in this reproduction period, and each female preferred to scrounge from a different set of males with little overlap. Specifically, the overlap between the preferences of each two females in this network (i.e., between two sets of four preferred males) was 1.2 males (of the 4 preferred males) on average, which is not significantly different from a random assignment of preferred males (a random assignment results in an overlap of 1.1 males; $p = 0.23$; permutation test). When considering all adult males, there was also no correlation between the male preferences of any two females (Spearman correlation; not significant [n.s.] or negative correlation for all females; see STAR Methods).

Moreover, being a very consistent food collector does not seem to influence a male's reproductive success. We found no significant difference between the producing tendency of reproductive males and non-reproductive ones during the monitoring period (Figure 2; $p = 0.18$, permutation test; producing tendency was measured as the normalized ratio of the producing to scrounging events of an individual, which we term the producer index; see STAR Methods). Just like the relative producing tendency, the total amount of a male's producing also did not predict its mating success: males that sired offspring did not produce significantly more than males that did not sire any ($p = 0.82$; permutation test). Unlike the scrounging specificity (see above), the total amount of producer-scrounger interactions between parents was not significantly different from that of random male-female pairs ($p = 0.08$; permutations over father identities; compare with $p = 0.001$ for the scrounging specificity described above), which further consolidates the importance of scrounging specificity over the actual amounts of transferred food.

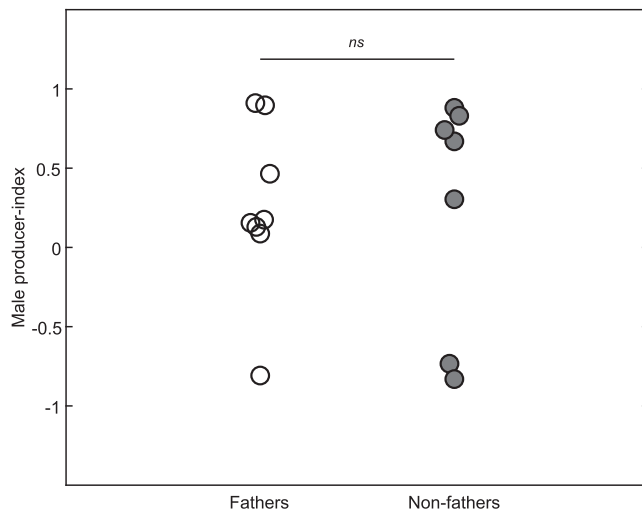


Figure 2. Male Producing Tendency Is Not Associated with Reproductive Success

Producer index (PI), the relative difference between the producing and scrounging actions of an individual (see STAR Methods), did not differ between reproductive males (empty circles, mean PI = 0.17) and non-reproductive males (gray circles, mean PI = 0.43) during the monitoring period ($p = 0.18$; permutation test).

Interestingly, examining the parenting bonds over six reproduction seasons suggests that male-female pairs usually switch between seasons. The 18 pups for which we could determine paternity over the six seasons were born to 8 females (two females had four pups each, one female had three pups, two females had two pups each, and three females had one pup each). Note that females always gave birth to (no more than) a single pup in a mating season. Twelve males fathered these 18 pups, and although five females reproduced more than once, there was not even a single case of the same parental pair reproducing more than once (Figure 3). This indicates negligible pair fidelity across mating seasons. To illustrate how unexpected this random male-female binding is, we consider a scenario in which each female is faithful to only six preferred males (half of those who reproduced), choosing randomly between them in each season. Even in this extremely random case, we would still expect at least one repeating parental pair to occur in our data (the pattern we observed, i.e., the number of recurrent pairs in these conditions, was thus significantly lower than expected by chance, $p < 0.03$, exact test, keeping the number of pups for each female fixed). More promiscuous situations, in which females choose randomly from even a larger group of preferred males, are slightly more likely to give rise to such a scattered pattern of paternity (Figure S1).

Scrounging Specificity among Parents Is Strongest around the Mating Period

Females, which normally scrounged food mostly from males, increased this bias even more in the month before their conception (Wilcoxon signed rank test: $p = 0.047$; Figure S2; see STAR Methods for details). Furthermore, we have previously found in another colony that producer-scrounger interactions are more selective around mating [23]. Additionally, using the genetic

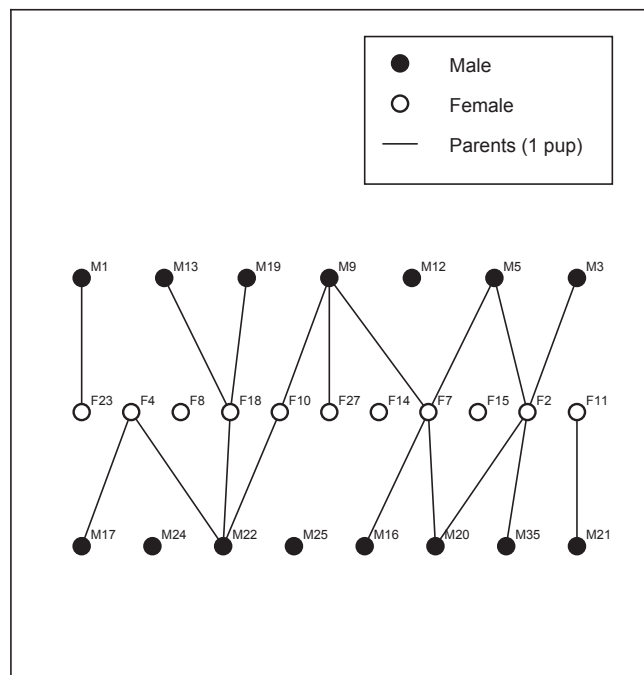


Figure 3. Infidelity across Mating Seasons among Reproductive Pairs

All parents identified in this study are depicted. The order in this layout is meaningless. Males, black circles; females, white circles. An edge between a male and a female represents a productive sexual relation in one season, which produced a single pup. Each female gives birth to at most one pup in a mating season (~6 months apart). We have not identified a single reoccurring pair of parents, even though five females gave birth more than once. The figure includes all adult bats (15 males and 10 females) and female F27, which was a juvenile during the monitoring period and gave birth toward the end of the genetic sampling (a year after the end of the monitoring period). See also Figure S1.

data of all 17 pups for which the exact birth date was known, we could identify the scrounging specificity of each parental pair during a period starting ~2 years before mating in some cases and until ~1 year after mating in other cases. We found that the highest scrounging specificity was formed around the time of conception, i.e., 120–140 days before each pup's birth date (Figure 4; compare with the association of each parent with other adult bats). Note that the scrounging specificity of the parents fluctuates periodically with a period of ~1 year (see the two lower peaks in Figure 4, depicted by arrows, 1 year apart from the main peak). This observation suggests that reproducing pairs intensify their relationship every reproduction season but that their producer-scrounger specificity reaches a peak only during a season when they reproduce. This periodic behavior is coherent with our previous findings regarding the general cyclic nature of the producer-scrounger associations in the colony [23].

DISCUSSION

In the research of the evolution of sociality, intersexual exchanges of benefits are often a fertile ground for speculations. The food-for-sex hypothesis, namely the provision of females

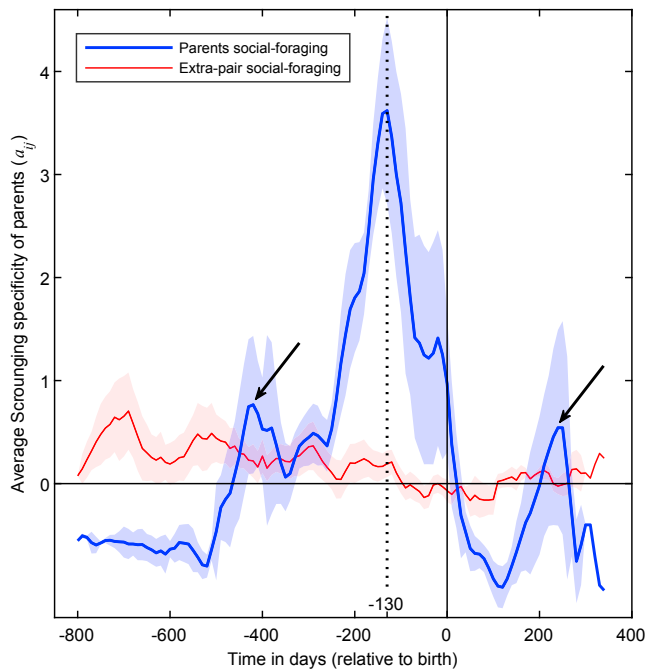


Figure 4. Parents Scrounging Specificity Relative to Pup's Time of Birth

For each pup, a sliding window was used in order to measure the scrounging specificity among its parents at different times relative to its birth (time zero; see STAR Methods). The blue line depicts the average of the values for the different pups, computed for each pup in bins of 10 days. Each pup contributed data to a ~500-days segment (i.e., the monitoring period, relative to the pup's birth). For comparison, the red line depicts the extra pair scrounging specificity. This is the mean of all scrounging-specificity scores of all reproductive females except of the pup's mother toward the pup's father and the scrounging specificity of its mother toward all reproductive males except its father. Shaded area depicts SEM (last part with no shade represents data of only one pup). Note the maximum at 130 days before birth, marked with a vertical dashed line (the gestation of *R. aegyptiacus* lasts approximately 120–140 days). Also note the secondary peaks, exactly 1 year later and ~10 months earlier to birth (depicted by black arrows), exemplifying periodic seasonal social interactions. See also Figures S2 and S3.

by males in return for mating opportunities, has been suggested to act in instances of intersexual cooperation and to serve as a driving force of sexual selection. In this study, we have found strong evidence for such relationships in a bat colony. Testing the correspondence between social foraging and reproduction is often tricky. Certain levels of female control over conception, whether physiological or through mating with others, may hinder the detection of the ultimate exchange of goods. Furthermore, it is not always straightforward for researchers to continuously track mating events. In this study, we bypassed these obstacles by directly testing the paternity of pups born in the colony using a genetic analysis. This test revealed a strong relationship between producer-scrounger interactions and reproduction. Specifically, females bore pups of the males from which they often scrounged food. Moreover, a bird's-eye analysis of the timing of producer-scrounger interactions between reproductive pairs showed a clear peak around the time of conception (Figure 4). This finding consolidates the relation between food-related interactions and sexual activity.

Several hypotheses have been suggested to explain exchange of food between reproducing pairs. Nuptial gifts, in the form of food being transferred from the male to the female right before or during copulation, are common in many invertebrates [25]. They are often believed to provide significant nutritional benefits to the female and thus to increase the reproductive success of both sexes [26]. In our case, however, the direct nutritional benefits from the food sharing are probably of little significance to the females, because when their energetic demands increase, e.g., during lactation [27], the females become more producers and less scroungers [23]. On the other hand, it is worth noting that, during gestation, the scrounging specificity between the future parents is still relatively high (see Figure 4; between conception and birth). Whether this pattern indeed reflects some added nutritional support is yet to be determined in further research. Nuptial gifts have also been suggested to prolong the mating and increase its success rate. In our species, however, the producer-scrounger interactions are separated from the copulation itself in time and mostly also in place. In a previous study, we showed that producer-scrounger interactions were not mediated by individual spatial preference [23]. Furthermore, in the bat colony, reciprocity between foraging and mating was not immediate but rather occurred over an extended period of time. Explicitly, the producer-scrounger associations between future parents began weeks or even months before the successful copulation (Figure 4) and the copulation itself typically does not occur during feeding times but hours later. The fact that the bats construct and maintain a dynamic social map, which relies on individual recognition and assessment of the cooperation of multiple peers over long time periods, enabled the delayed reciprocity. Such phenomena (in a non-mating context) were also observed in blood-sharing vampire bats [9, 28].

A simpler account for the prevalent producer-scrounger interactions between bats could have been that of a “tolerated theft,” in which the costs of protecting a food item are larger than the benefits of maintaining it. However, because there was a strong correlation between scrounging specificity and reproduction in the colony, this is probably not the main explanation for the observed producer-scrounger interactions.

Another commonly suggested explanation for the appearance of food-sharing behaviors is that they serve as a “costly signaling” of the male qualities. For example, nuptial gifts in birds occasionally serve as part of the courtship [25, 29]. More commonly, birds use vocal signaling during courtship. Indeed, also in some species of bats, males advertise their quality using courtship or territorial songs [30, 31], similarly to songbirds [32]. A leading hypothesis is that these signals convey information about the singer's strengths as it risks exposure or demonstrates vocal virtuosity [33–35]. Egyptian fruit bats demonstrate a highly complex and flexible vocal communication system [36–38], but they do not use advertisement songs and in fact rarely use any kind of broadcast vocalizations [24]. Thus, the sharing of food might replace the song system and serve as a “costly signal” [4] for male quality in this species. Importantly, in the wild, collecting food items may impose several types of costs on the producer bat, including the energy spent while searching for, and harvesting, ripe fruits; the competition over available food on a specific tree; and the risk of predation during landing on and

handling an exposed fruit. Indeed, in the past, we showed a strong correlation between risk taking and producing [23]. However, in this study, we have found no correspondence between the production ability (the absolute production or the relative production; Figure 2) and the reproductive success of males. Furthermore, we have not found any male that has prevailed over all others in siring offspring, suggesting that no superior quality has been advertised during the foraging interactions. Thus, costly signaling might be speculated to play some role in the intersexual producer-scrounger interactions, but it is probably not a main factor.

Following the discussion above, we hypothesize that the observed relation between food scrounging and mating is a form of mutualism exhibited in delayed reciprocity: scrounging food from a successful male forager diminishes the costs of foraging and is compensated, if consistent over time, by rewarding the male with mating opportunities. In addition to direct nutrition, food sharing might contribute to reducing predation risk. Landing on a fruit tree makes the bat more sensitive to predation, and landing near an individual (a male) that has already obtained fruit reduces the risk for at least two reasons: first, it suggests that there is no predator lurking in the tree and, second, producers typically carry the fruit to a nearby safe tree. Indeed, in the past, we have demonstrated a strong correlation between hesitance and scrounging [23]. Some suggested to interpret such relationship as pseudo-reciprocity [39], as the female benefits both from the food sharing and from mating a successful male. Interestingly, however, not the absolute food transfer between the pair but their relative association predicted a pair's parenting in this study, i.e., females reproduced with males that were specifically associated with them. This mutualism requires repeated interactions over extended time periods. Long-term relationships, as those observed in Egyptian fruit bat colonies (wild and captive), provide opportunity for such delayed reciprocity.

A close look at the changes of the scrounging specificity among reproductive pairs revealed periodic annual fluctuations (arrows in Figure 4). These oscillations are coherent with our previous finding that the producer-scrounger bonds in the colony are persistent, to some extent, with higher correlation between similar periods along the reproduction cycle [23]. That is, the specificity during a mating season was found, in that study, to be partially correlated with the specificity of the previous and next mating seasons.

Interestingly, our colony exhibited an egalitarian sociality, with no signs of dominance in foraging or mating interactions. Each female held an individualistic set of preferred males from whom she scrounged food (with little overlap between females). This set appeared to gradually change over seasons, where males could also shape their affiliation with specific females according to their tendency to share food. These results, together with the lack of correlation between males' production and reproductive success, exclude possible biases that might be introduced when examining the food-for-sex hypothesis, due to dominance of some of the males (i.e., that a few males provide the food to everyone and also father all the pups).

The long-term genetic monitoring of pups also revealed extreme infidelity across mating seasons, as no two pups were born to the same pair of parents. In fact, our findings suggest that, although the seasonal pairing is constructed through

repeated producer-scrounger interactions, the choice of the partners varies between seasons in such an extent that might even exceed the expected variation of random pairing (Figure S1). We can only speculate that either some mechanism acts in favor of diversification or, alternatively, that the bats possess a high level of promiscuity, which does not even include a small constant set of preferred male partners.

To conclude, the genetic-based evidence for intersexual reciprocity in foraging and mating tighten our understanding of the social life of bats and mammals in general. Bats appear to possess elaborate social-cognitive skills allowing them to construct an organized society, though fluid and not hierarchical, in a dense, non-territorial, and durable social environment.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- KEY RESOURCES TABLE
- CONTACT FOR REAGENTS AND RESOURCE SHARING
- EXPERIMENTAL MODEL AND SUBJECT DETAILS
- METHOD DETAILS
 - Data collection and experimental procedure
 - Tissue sample collection
 - Molecular methods and genetic analyses
- QUANTIFICATION AND STATISTICAL ANALYSIS
 - Scrounging-specificity
 - Change in time of scrounging-specificity among parents
 - Producer-Index (PI)
 - Statistical analysis

SUPPLEMENTAL INFORMATION

Supplemental Information can be found online at <https://doi.org/10.1016/j.cub.2019.04.066>.

ACKNOWLEDGMENTS

We thank Liran Samuni for insightful comments on an earlier version of this manuscript. This research was partially supported by the European Research Council (ERC-2015-StG - 679186_GPS-Bat).

AUTHOR CONTRIBUTIONS

L.H. and Y.Y. designed the experiment; Y.P., L.H., and Y.Y. conceived the analysis; L.H. conducted the experiment; and Y.P. conducted the analysis. S.B.C. and R.D. performed the genetic analysis. Y.P. and Y.Y. wrote the manuscript, and L.H., S.B.C., and R.D. reviewed it. L.H. and Y.P. contributed equally to this work.

DECLARATION OF INTERESTS

The authors declare no competing interests.

Received: January 23, 2019

Revised: March 21, 2019

Accepted: April 25, 2019

Published: May 23, 2019

REFERENCES

1. Hamilton, W.D. (1964). The genetical evolution of social behaviour. I. *J. Theor. Biol.* 7, 1–16.
2. Blurton Jones, N.G. (1984). A selfish origin for human food sharing: tolerated theft. *Ethol. Sociobiol.* 5, 1–3.
3. Gilby, I.C. (2006). Meat sharing among the Gombe chimpanzees: harassment and reciprocal exchange. *Anim. Behav.* 71, 953–963.
4. Zahavi, A. (1975). Mate selection—a selection for a handicap. *J. Theor. Biol.* 53, 205–214.
5. Zahavi, A. (1977). The cost of honesty (further remarks on the handicap principle). *J. Theor. Biol.* 67, 603–605.
6. Smith, E.A., and Bird, R.L.B. (2000). Turtle hunting and tombstone opening. public generosity as costly signaling. *Evol. Hum. Behav.* 21, 245–261.
7. Axelrod, R., and Hamilton, W.D. (1981). The evolution of cooperation. *Science* 217, 1390–1396.
8. Wilkinson, G.S. (1984). Reciprocal food sharing in the vampire bat. *Nature* 308, 181–184.
9. Carter, G.G., and Wilkinson, G.S. (2013). Food sharing in vampire bats: reciprocal help predicts donations more than relatedness or harassment. *Proc. Biol. Sci.* 280, 20122573.
10. Wilkinson, G.S., Carter, G.G., Bohn, K.M., and Adams, D.M. (2016). Non-kin cooperation in bats. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 371, 20150095.
11. Samuni, L., Preis, A., Mielke, A., Deschner, T., Wittig, R.M., and Crockford, C. (2018). Social bonds facilitate cooperative resource sharing in wild chimpanzees. *Proc. Biol. Sci.* 285, 20181643.
12. Trivers, R.L. (1971). The evolution of reciprocal altruism. *Q. Rev. Biol.* 46, 35–57.
13. Clutton-Brock, T. (2009). Cooperation between non-kin in animal societies. *Nature* 462, 51–57.
14. de Waal, F.B.M. (1989). Food sharing and reciprocal obligations among chimpanzees. *J. Hum. Evol.* 18, 433–459.
15. Kaplan, H., and Hill, K. (1985). Hunting ability and reproductive success among male Ache foragers: preliminary results. *Curr. Anthropol.* 26, 131–133.
16. Gomes, C.M., and Boesch, C. (2009). Wild chimpanzees exchange meat for sex on a long-term basis. *PLoS ONE* 4, e5116.
17. Dale, R., Marshall-Pescini, S., and Range, F. (2017). Do females use their sexual status to gain resource access? Investigating food-for-sex in wolves and dogs. *Curr. Zool.* 63, 323–330.
18. Kaplan, H., Hill, K., Cadeliña, R.V., Hayden, B., Hyndman, D.C., Preston, R.J., Smith, E.A., Stuart, D.E., and Yesner, D.R. (1985). Food sharing among Ache foragers: tests of explanatory hypotheses. *Curr. Anthropol.* 26, 223–246.
19. Smith, E.A., Bird, R.B., and Bird, D.W. (2003). The benefits of costly signaling: Meriam turtle hunters. *Behav. Ecol.* 14, 116–126.
20. Gilby, I.C., Emery Thompson, M., Ruane, J.D., and Wrangham, R. (2010). No evidence of short-term exchange of meat for sex among chimpanzees. *J. Hum. Evol.* 59, 44–53.
21. Kerth, G. (2008). Causes and consequences of sociality in bats. *BioScience* 58, 737–746.
22. Kerth, G., and VAN Schaik, J. (2012). Causes and consequences of living in closed societies: lessons from a long-term socio-genetic study on Bechstein's bats. *Mol. Ecol.* 21, 633–646.
23. Harten, L., Matalon, Y., Galli, N., Navon, H., Dor, R., and Yovel, Y. (2018). Persistent producer-scrounger relationships in bats. *Sci. Adv.* 4, e1603293.
24. Prat, Y., Taub, M., and Yovel, Y. (2016). Everyday bat vocalizations contain information about emitter, addressee, context, and behavior. *Sci. Rep.* 6, 39419.
25. Lewis, S., and South, A. (2012). The evolution of animal nuptial gifts. *Adv. Stud. Behav.* 44, 53–97.
26. Vahed, K. (1998). The function of nuptial feeding in insects: a review of empirical studies. *Biol. Rev. Camb. Philos. Soc.* 73, 43–78.
27. Korine, C., Speakman, J., and Arad, Z. (2004). Reproductive energetics of captive and free-ranging Egyptian fruit bats (*Rousettus aegyptiacus*). *Ecology* 85, 220–230.
28. Carter, G.G., and Wilkinson, G.S. (2015). Social benefits of non-kin food sharing by female vampire bats. *Proc. Biol. Sci.* 282, 20152524.
29. Lack, D. (1940). Courtship feeding in birds. *Auk* 57, 169–178.
30. Smotherman, M., Knörnschild, M., Smarsh, G., and Bohn, K. (2016). The origins and diversity of bat songs. *J. Comp. Physiol. A Neuroethol. Sens. Neural Behav. Physiol.* 202, 535–554.
31. Knörnschild, M., Nagy, M., Metz, M., Mayer, F., and von Helversen, O. (2010). Complex vocal imitation during ontogeny in a bat. *Biol. Lett.* 6, 156–159.
32. Catchpole, C.K., and Slater, P.J.B. (2003). *Bird Song: Biological Themes and Variations* (Cambridge University Press).
33. Bohn, K.M., Schmidt-French, B., Schwartz, C., Smotherman, M., and Pollak, G.D. (2009). Versatility and stereotypy of free-tailed bat songs. *PLoS ONE* 4, e6746.
34. Behr, O., and von Helversen, O. (2004). Bat serenades—complex courtship songs of the sac-winged bat (*Saccopteryx bilineata*). *Behav. Ecol. Sociobiol.* 56, 106–115.
35. Knörnschild, M., Behr, O., and von Helversen, O. (2006). Babbling behavior in the sac-winged bat (*Saccopteryx bilineata*). *Naturwissenschaften* 93, 451–454.
36. Prat, Y., Taub, M., and Yovel, Y. (2015). Vocal learning in a social mammal: demonstrated by isolation and playback experiments in bats. *Sci. Adv.* 1, e1500019.
37. Prat, Y., Taub, M., Pratt, E., and Yovel, Y. (2017). An annotated dataset of Egyptian fruit bat vocalizations across varying contexts and during vocal ontogeny. *Sci. Data* 4, 170143.
38. Prat, Y., Azoulay, L., Dor, R., and Yovel, Y. (2017). Crowd vocal learning induces vocal dialects in bats: Playback of conspecifics shapes fundamental frequency usage by pups. *PLoS Biol.* 15, e2002556.
39. Connor, R.C. (1986). Pseudo-reciprocity: investing in mutualism. *Anim. Behav.* 34, 1562–1566.
40. Kalinowski, S.T., Taper, M.L., and Marshall, T.C. (2007). Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. *Mol. Ecol.* 16, 1099–1106.
41. Andrianaivoarivelo, A.R., Shore, G.D., McGuire, S.M., Jenkins, R.K.B., Ramilijaona, O., Louis, E.E., and Brennehan, R.A. (2009). Characterization of 22 microsatellite marker loci in the Madagascar rousette (*Rousettus madagascariensis*). *Conserv. Genet.* 10, 1025–1028.
42. Hua, P.Y., Chen, J.P., Sun, M., Liang, B., Zhang, S.Y., and Wu, D.H. (2006). Characterization of microsatellite loci in fulvous fruit bat *Rousettus leschenaulti*. *Mol. Ecol. Notes* 6, 939–941.

STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Experimental Models: Organisms/Strains		
Egyptian Fruit-bat, <i>Rousettus aegyptiacus</i>	Wild	N/A
Biological Samples		
3-mm-diameter wing punches from Egyptian Fruit-bat, <i>Rousettus aegyptiacus</i>	Wild	N/A
Software and Algorithms		
MATLAB 9	MathWorks	MATLAB 9
Cervus v3.0.7	[40]	http://www.fieldgenetics.com/pages/aboutCervus_Overview.jsp
GeneMarker v2.6.7	SoftGenetics	https://softgenetics.com/GeneMarker.php
Oligonucleotides		
Primers for genotyping, see Table S1	[41, 42]	N/A
Critical Commercial Assays		
DNeasy Blood & Tissue Kit	QIAGEN	Cat# 69504

CONTACT FOR REAGENTS AND RESOURCE SHARING

Further information and requests for resources and reagents should be directed to and will be fulfilled by the Lead Contact, Yossi Yovel (yossiyovel@gmail.com).

EXPERIMENTAL MODEL AND SUBJECT DETAILS

The captive colony consisted of 34 Egyptian fruit-bats (*Rousettus aegyptiacus*). 25 mature individuals (15 males and 10 females), which are included in the main analysis (Figures 1 and 3), 8 juveniles (2 males, 5 females, 1 unknown), and one adult female which died during the experiment. The adult bats were all caught at the same roost (32°10'5.41"N, 34°48'51.33" E, ca. 1 year apart). This is a huge *R. aegyptiacus* colony with at least 6000 individuals spread within multiple compartments. At each capture, we made sure to distribute the capture in time and space; namely, the bats were collected along 1 hour from different locations in the cave. Moreover, once we entered the cave, a commotion started, with bats flying all over the place, so the probability of collecting two related bats or two bats from the same original cluster was very low. Genetic analysis confirmed that this strategy resulted in capturing unrelated adults [23]. The colony was housed and observed in an indoor aviary (2 m × 4 m × 3 m) with a naturally fluctuating day/night cycle and access to an outdoor meshed aviary via a single open window. All experiments were performed with permission from the Tel Aviv University Institutional Animal Care and Use Committee (number L-12-039, L-15-031).

METHOD DETAILS

Data collection and experimental procedure

Two observers carried out observations of foraging bouts. Observations began once all bats had dispersed from the sleeping cluster. Before each observation bout, a bowl containing slices of banana (ca. 400 g) was placed on a podium (ca. 1 m high) in the center of the enclosure. Each observation session lasted approximately 40 min because this was the period needed for the bats to deplete the bowl. All foraging events, defined as any food acquisition by an individual, were scored. Foraging events were then categorized as either producing or scrounging events, with food collection from the bowl noted as a producing event and approaching behaviors to the producer's mouth denoted as scrounging events (these occurred on average within 0.8 min from the producing event, see also Video S1). The colony was observed ca. twice a week (a total 104 days) from March 2015 to July 2016, with a total of 220 hours of observation. Overall 8179 foraging records were collected (producing-scrounging and producing without scrounging).

Tissue sample collection

We sampled two 3-mm-diameter wing punches from pups that were born in the colony between May 2015 and November 2017 and from adults. Aborted fetuses were also sampled and are considered as "pups" to this end. Out of 24 pups that were sampled we could identify both parents for 18 pups (13 born alive and 5 aborted fetuses; for one of them the birth date was unknown), and these

were included in the analysis. Two punches per individual were preserved in molecular grade 100% ethanol and frozen at -80° . Wing tissues were obtained using sterile, disposable 3-mm skin biopsy punches. One biopsy punch was used per individual, and the samples were taken from regions of the wing that were far enough from major blood vessels and the edge of the wing to avoid tearing.

Molecular methods and genetic analyses

Genomic DNA was extracted for all adults and pups in the colony using DNeasy tissue Extraction kit (QIAGEN). Samples were genotyped at 10 microsatellite marker loci developed for *Rousettus madagascariensis* [41] or *Rousettus leschenaulti* [42] using conditions described in Table S1. Amplified products were visualized on an ABI 3100 genetic analyzer. Allele size scoring was performed using GeneMarker v2.6.7 (SoftGenetics, LLC), verified, and amended by eye. We examined the deviation from Hardy-Weinberg equilibrium (HWE) and the presence of null alleles using the software Cervus v3.0.7 [40]. Microsatellite markers were polymorphic (mean allele number per locus, 6.8; range, 5 to 9), did not deviate from HWE, and had a low level of null alleles ($< 15\%$). We assigned paternity using methods implemented in Cervus v3.0.7 [40], while the mother identity was usually also known due to the maternal care (carrying the pup). The combined exclusion probability for the first parent was 0.98622, for the second parent 0.99939, and for the parent pair 0.99999. We compared manually the genotypes of the potential parents suggested by the software to the genotypes of the pups in order to ensure correct assignments, and excluded other potential parents.

QUANTIFICATION AND STATISTICAL ANALYSIS

Scrounging-specificity

The (directed) scrounging-specificity of each bat i toward bat j (a_{ij}), was computed as the deviation of scrounging events (of bat i from bat j) from the expected number of events:

$$a_{ij} = \frac{S_{ij} - \mu_{ij}}{\sigma_{ij}} \quad (1)$$

The expected number of such events (μ_{ij}) and the corresponding standard-deviation (σ_{ij}) were approximated using the binomial mean and variance:

$$\mu_{ij} = N \cdot \text{Prob}(s=i, p=j) \quad (2)$$

$$\sigma_{ij} = N \cdot \text{Prob}(s=i, p=j) \cdot (1 - \text{Prob}(s=i, p=j)) \quad (3)$$

where $\text{Prob}(s=i, p=j) = \text{Prob}(s=i | p=j) \text{Prob}(p=j)$ is the probability of observing bat i scrounging from bat j given only the propensity of each of the bats to scrounge or produce. The probabilities of each bat in the colony to act as a producer (p) or a scrounger (s) were estimated using the empirical occurrences of such events (with $|\cdot|$ meaning the number of events):

$$N = |\text{all production events}|$$

$$\text{Prob}(p=j) \triangleq \frac{|p=j|}{N} \quad (4)$$

$$\text{Prob}(s=i | p=j) \triangleq \frac{|s=i|}{N - |s=j|} \quad (5)$$

the denominator of Equation (5) includes all N production events since it includes all scrounging, and also the production events which ended with no scrounging (i.e., $\text{Prob}(s = \text{none}) > 0$). It excludes all scrounging of bat j since, also in our null model, bat j cannot scrounge from itself. Accordingly, we set $\forall j \text{ Prob}(s=j | p=j) = 0$.

Change in time of scrounging-specificity among parents

To study the temporal nature of the specificity among pairs of bats which were identified as parents, we calculated their scrounging-specificity using a sliding window. For each pair (of parents) we measured the scrounging-specificity of the female toward the male in a window of 120 days, sliding in steps of one day (shorter windows yield the same results with more noise, due to less data; see Figure S3). We aligned the obtained measurements of all parents (using the genetic analysis of all 17 pups) according to the birth date of their pup (i.e., 0 is the birth date of the pup; the exact birth-date of one of the 18 pups was unknown, thus it was not used in this analysis). Then, the graph in Figure 4 was produced by calculating the mean of each pup in bins of 10 days (each bin contains 10 points for each pup, as the sliding step is one day, and the binning allows alignment of all participating pups in each window). This analysis shows a conspicuous maximum at 130 days before birth.

Producer-Index (PI)

The producer-index of bat i is computed as the relative-difference between its producing and scrounging actions:

$$PI_i = \frac{p_i - s_i}{p_i + s_i}$$

Where p_i is the number of producing events of bat i (i.e., number of times another bat scrounged from bat i) and s_i is the number of scrounging events of bat i . The range of PI is between -1 (a pure scrounger) and $+1$ (a pure producer).

Statistical analysis

The significance of the difference between scrounging-specificity of parents and non-parental pairs (Figure 1A), was evaluated by calculating the scrounging-specificity of the eight reproductive pairs (parents to pups that were conceived during the monitoring period). We then compared this mean-score to 100,000 mean-scores of eight randomly sampled female-male pairs, obtaining a p -value of 0.0013. When sampling the pairs, we held the number of pups for each female constant (i.e., we kept the sums of the rows in the paternity-matrix the same). If we hold the number of pups for each male constant as well (i.e., we also keep the sums of the columns in the paternity-matrix the same), the p -value is much lower ($p = 0.0001$), but since we have no strong basis to assume that males are extremely limited in the number of pups they can produce in a mating season (one pup in this case), we do not use the latter test. Note that since the paternity-matrix is binary, this permutation test is equivalent to a Mantel test for the correlation between the scrounging-specificity and paternity networks. This test was performed using 15 males and the 7 females which gave birth during the monitoring period (one gave birth twice). Even the strictest test, sampling only from the eight fathers (and not all 15 males) results in a p -value < 0.0025 . Using the total number of producer-scrounger interactions, instead of scrounging-specificity, for testing the relationships of the eight reproductive pairs against random pairing in the same manner, results in non-significant p -value of 0.08 (compare with 0.0013 for scrounging-specificity).

Bias of females-scrounging toward males was measured as the fraction of scrounging from males out of all scrounging events for each female, which gave birth during the monitoring period. Difference between this bias during pre-mating and all other times was evaluated using Wilcoxon signed-rank test (Figure S2). Pre-mating period was considered as 160-120 days before the birth of the pup.

To evaluate the significance of the relation between productivity (producer-index, PI) and reproductive success we performed an (exact) permutation test (i.e., by testing all 6435 permutations of father/non-father labels, with 8 fathers among 15 adult males).

We measured the correlation between the male-preferences of each possible pair of the 10 mature females. To this end, we considered the vector of scrounging-specificity scores of each female with all the adult males. We then searched for significant positive Spearman correlation between any pair of these vectors. We found no such pair of females ($p > 0.05$ for any possible two females), i.e., each female had an individualistic set of male-preferences.

All analyses were conducted using MATLAB 9.